

Diet and isotopic metrics of predatory and prey fish in two estuaries with different degrees of anthropogenic disturbances: the case study of Wami and Pangani rivers in Tanzania

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ABSTRACT

Diverse anthropogenic activities including alteration of hydrological regime and agricultural development in the upstream of the river catchments modify the structural components of communities and ecological roles of species in estuarine ecosystems. The present study compared the diet, carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios and Layman community metrics of predatory fish and their prey-fish between two estuaries with different degrees of anthropogenic disturbances. The Layman community metrics were estimated following the Bayesian approach. It was revealed that the diets of the predators *Arius africanus*, *Epinephelus coioides*, *Sillago sihama* and *Pomadasys argenteus*, and their isotopic values including their main prey, the fish *Valamugil buechanani*, were significantly different between Wami and Pangani estuaries (PERMANOVA, Pseudo- $F \geq 3.1$, $p=0.05$). The comparison test of isotopic niche width at estuary level showed that the isotopic niche of Wami estuary was slightly narrower (3.90-6.94 at 95% CI) than that of Pangani (5.70-9.69 of 95% CI). The comparison of the $\delta^{15}\text{N}$ values and range of species between estuaries suggest shifts in trophic position of the species in Wami estuary relative to that of Pangani. Furthermore, the Layman metric indices of trophic diversity and redundancy of Wami estuary were substantially smaller, when compared to that of Pangani estuary. These findings indicate that, even though the Wami estuary stands under a conservation status, the extent of disturbances in the upstream is potentially high and enough to induce the ecological changes at the base of the food web downstream, giving rise to subsequent effects transmitted to higher-order consumers. As a result, the ecological redundancy and ecosystem complexity of Wami are possibly compromised relative to that of Pangani estuary.

INTRODUCTION

Estuaries are among the most biologically productive and economically valuable ecosystems in the world. The hydrological regime and geomorphological features of estuaries make such ecosystems good shelters, feeding and breeding grounds for many marine fish species at various stages of their life cycles (Beck *et al.*, 2001; Pihl *et al.*, 2002; Harrison and Whitfield, 2006; Kostecki *et al.*, 2010; Selleslagh *et al.*, 2015). Estuaries provide essential and complex habitats to sustain different freshwater and marine fish stocks. The estuarine complexity provides juvenile fishes with adequate protection from predation while attaining high growth rates supported by a high primary productivity (Kostecki *et al.*, 2010; Whitfield, 2016). Nevertheless, the ecological status of most estuaries is threatened due to modifications made by anthropogenic activities. Estuaries are subjected to increasing human pressure through urbanization, overfishing and upstream catchment disturbances resulting from deforestation, water abstraction for reservoir or multi-dams construction and water diversion for irrigation activities (Abrantes *et al.*, 2014).

The physical, chemical and biological characteristics of estuaries are dynamic both on temporal and spatial scales (Selleslagh *et al.*, 2015). The main drivers of such

fluctuations are hydrological regimes, encompassing freshwater discharges from the upstream, coastal wave activity and tidal water flow at the mouths of the estuaries (Gillson, 2011; Hoeninghaus *et al.*, 2011). The interference of such hydrological regime such as upstream water abstraction for irrigation and damming for hydropower generation causes retention and thus reduction of nutrients, sediment (that serve as an ecological niche to some species), quantity and quality of organic matter reaching the estuary (Han *et al.*, 2016). Variations in the hydrological regime impact habitat availability and diversity, primary production, trophic interactions and consequently prompt responses in food web structure and functioning (Gillson, 2011; Whitfield, 2016; Donázar-Aramendía *et al.*, 2019). More so, the regulation of the flow rate of freshwater reaching the estuaries greatly influences the diversity of basal organic matter fueling the estuarine food webs (Abrantes *et al.*, 2013).

Juvenile marine fish with predatory behavior constitute a great part of estuarine fish communities. They are highly targeted by local or artisanal fisheries while still at juvenile and sub-adult stages, as they attain large body sizes before reaching maturity (Shaw *et al.*, 2016; Mwijage *et al.*, 2018a). As such, they have lucrative market price when compared to the small fish that feed at lower trophic levels. Predatory fish and other higher order consumers coexist

in estuaries as they exert reciprocally positive indirect effects by regulating the populations of their respective preys, and in that way, prevent competitive exclusion of each other's preys (Sanders *et al.*, 2018). They also link pelagic, benthic and detritivore food webs in estuarine ecosystems through predator-prey interactions (Rooney and McCann, 2012). Because of the array of ecological roles they play, by studying these predators, one can get insights into the role of predatory fish for maintaining the structure and functioning of estuarine ecosystem.

The Pangani and Wami River estuaries are situated about 55 kilometers apart in the coastal northern part of Tanzania. The Pangani estuary is managed by Pangani Water Basin Office Authority, and thus it is an open access estuary. The Wami estuary is part of Saadani National Park (SANAPA) and is therefore a protected estuary but the whole river is managed by Wami-Ruvu Water Basin Office Authority. However, the upstream part of Pangani and Wami rivers are subjected to different anthropogenic activities that may be affecting the ecology of estuarine fish and other biota in different ways. In the upstream portion of Pangani catchment, water is mainly abstracted by multi-damming for hydroelectric power generation and irrigation (Shaghude, 2016; Mwijage, *et al.*, 2018a). The retained sediments and organic particles in the reservoirs and the elevated load of nutrient inputs arising from these activities affect different ecological processes downstream the rivers including estuaries. Yet, water upstream of Wami estuary is widely used for fishing and irrigation in rice paddies and commercial sugarcane plantations (Eeden and Koppen, 2016).

There is an indication that the multi-damming activities in Pangani catchment have reduced the nutrients loading downstream (Selemani *et al.*, 2017) and caused some predatory fishes to largely rely on the estuarine and marine organic matter sources (Mwijage *et al.*, 2018a). In the Wami estuary, the basal primary food sources sustaining the components of the estuarine food webs is unknown. Despite the fact that the Wami estuary receives elevated nutrients and suspended particles from the upstream, according to Kiwango *et al.* (2015), the estuary is still ecologically healthy. Generally, the anthropogenic disturbances of Tanzanian estuaries and coastal ecosystem is high (see, *e.g.*, Semba *et al.*, (2016) and Shaghude (2016)), but little is known about the implications of such disturbances on the trophic niche, and other related dynamics, of fish assemblage and, consequently, on the entire estuarine ecosystem.

This paper aims at getting more insight into the above-mentioned perspectives, by comparing the diet and other trophic dynamics of fish species at the different degrees of anthropogenic disturbances present in Wami and Pangani estuaries. Stable isotopes and stomach content analyses are employed in complementarity to describe the

trophic structure in numerous ecosystems. Stable isotopes ratios of carbon ($\delta^{13}\text{C}$) and nitrogen $\delta^{15}\text{N}$ can be used as a robust tool to evaluate changes in the diet of native species in relation to the expansion of invasive species (García *et al.*, 2020). Stable isotopes are also used to analyze the trophic niche, dietary overlap and other trophic dynamics of food web components across varied ecosystems (Layman *et al.*, 2012; Jackson and Parnell, 2016; Gutmann and Britton, 2018; Wang *et al.*, 2018; Zhang *et al.*, 2019). Through the Bayesian framework, Layman metrics are estimated to enable evaluation of the numerous human-induced impacts on food webs, including ecological redundancy, resilience, diversity and trophic stability of ecosystems (Rooney and McCann, 2012; Matich *et al.*, 2017; Donázar-Aramendía *et al.*, 2019).

In this study, we examine the degree of dietary and isotopic niche flexibility of predatory fish and their phyto-detritivore prey-fish in the adjacent estuaries of Wami and Pangani rivers. Specifically, our study intended to (i) assess the extent of similarity or overlaps in diet of predatory fish; ii) estimate isotopic values and trophic niche of predatory fish and their phyto-detritivore prey-fish populations; and (iii) elucidate the status of complexity, resilience and redundancy of two estuarine ecosystems using Layman metrics. In presenting and discussing our results, we provide critical information to further understand the effects of the anthropogenic activities on fish communities and the resulting impacts on the Tanzanian river ecosystems as well as refine management approaches for sustainability of riverine and coastal resources in general.

METHODS

Study area

The study sites were based in the two macro-tidal estuaries of semi-diurnal type adjacent to each other, located in the northern coastal part of Tanzania, namely, Wami and Pangani estuaries (Figure 1). Both estuaries are permanently open, connected to the sea. The Wami estuary is part of the Saadani National Park (SANAPA) which was established in 2005 and thus, it is strictly protected. The tidal range in this estuary reaches up to 4 m during spring tides and the influence may extend up to 8 km upstream (Kiwango *et al.*, 2018a). During the wet season, the freshwater plume of Wami River extends for several hundred meters into the Indian Ocean during both low and high tides. Only the first five kilometers from the shore are occupied by mangroves. The estuary shows turbidity ≥ 400 NTU and suspended sediment concentrations of < 100 mg L⁻¹ during the dry season, and > 800 mg L⁻¹ during the wet season (Kiwango *et al.*, 2018a). A salt wedge is common in the offshore areas of Wami, several hundred

meters from the mouth of the river in a northeasterly direction. The Pangani estuary is located further north of Wami estuary (Figure 1) with a wave amplitude of about 3.5 m during the spring tides and 3.0 m at neap tides (Mwijage *et al.*, 2018a). The estuary extends to about 20 km from the estuary mouth (Mwijage *et al.*, 2018a). It has an extensive mangrove forest interspaced with coconut/palm trees. Pangani estuary experiences strong mixing of fresh and saline water. The hydrological regime is mainly regulated by the multi-reservoirs upstream of the catchment. Moreover, both estuaries serve as breeding and nursery grounds for marine fish, prawns, and birds, and they are known as the most productive areas of prawns for Tanzania. Wami estuary, to a larger extent, hosts a larger number of hippopotamus and crocodiles compared to those occurring in the Pangani estuary.

Field sampling procedures of fish

Fish samples were collected in Wami and Pangani River estuaries in July 2019 during the daytime. July is a

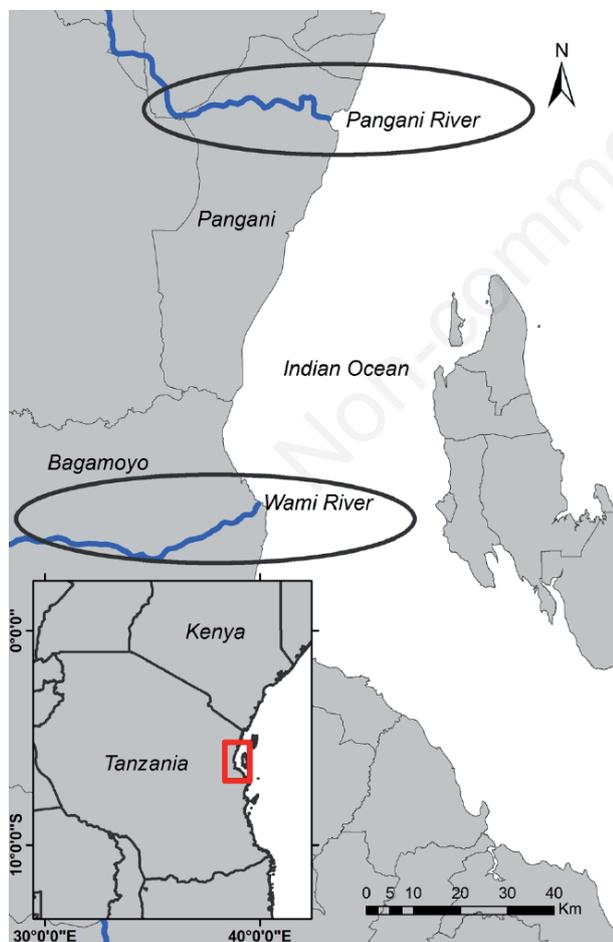


Figure 1. Map of Wami and Pangani river estuaries showing the study area.

dry-season month and within the peak of the southeast monsoon. Thus, field sampling was conducted after the peak of the rainy season which usually occurs in May; this allowed to reduce seasonal biasness by capturing isotopic values that would reflect dietary sources that were consumed by fish during the wet and dry seasons. This is based on the premise that isotopic values of consumer tissues indicate their long-term assimilated diet of at least three months. Fish species were caught by using monofilament gill nets of multiple mesh sizes and seine net with the dimensions of 15 m length, 1.5 m width and mesh size 0.5 mm. From the total landing, five abundant predatory fish species, namely *Arius africanus* (Günther 1867), *Epinephelus coioides* (Hamilton, 1822), *Sillago sihama* (Forsskål, 1775) and *Pomadasys argenteus* (Forsskål, 1775), and their main potential prey such as the phyto-detritivore *Valamugil buchanani* (Bleeker, 1853), were selected to study their trophic niches flexibility. The selection was based on what predatory fish species of marine affinity are abundant throughout the seasons (Bianchi, 1995; FIU-GLOWS, 2016).

Notably, marine fish species inhabiting Wami estuary include *A. africanus*, *V. buchanani*, *Chanos chanos*, *Ambassis gymnocephalus*, *Hilsa kelee*, *Thryssa spp.*, *Leiognathus equulu*, *Pomadasys spp.*, *Epinephelus spp.* and Tetraodontidae, (Anderson *et al.*, 2007; FIU-GLOWS, 2016). However, the diversity and abundance of these species decrease sharply as the distance from the mouth of the river to the upstream increases (FIU-GLOWS, 2016). In Pangani estuary, fish species with a marine origin commonly seen include *C. chanos*, *A. gymnocephalus*, *Gerres filamentosus*, *V. buchanani*, *Lutjanus argentimaculatus*, *sillago sihama*, *Epinephelus spp.* and species from the families of Sphyraenidae, Hemiramphidae, Gobiidae and Carangidae (PWBO/IUCN, 2008; Bianchi, 1995; Mwijage *et al.*, 2018a).

During the sampling, the predatory fish species *E. coioides* and *A. africanus* were caught in both estuaries along with their main prey, *i.e.*, *V. buchanani*. Both *S. sihama* and *P. argenteus* were abundantly caught in Pangani estuary, while *P. argenteus* was greatly caught within the plume setting at short distance from the mouth of the Wami estuary. Since the two above-mentioned species are classified as zoobenthivore under the feeding mode functional grouping (Elliott *et al.*, 2007), their trophic requirements are equivalent. Due to that, we decided to select them as another pair of comparison between estuaries. To get enough samples for stomach content analysis, additional samples of *P. argenteus* were bought from the local market immediately after being landed by local fishermen. All fish species caught were stored in ice boxes containing dry ice immediately after collection. Later, total length and weight were recorded, and all fish samples frozen at -20°C on the same day and transported to the

laboratory at the University of Dar es Salaam, College of Agricultural Sciences and Fisheries Technology for further analyses.

Fish stomach content analysis

In the laboratory, stomachs of all fish species caught were extracted and subjected to content analysis. The fish stomachs were dissected under a microscope to enable the determination of the frequency of occurrence (%FO) and percentage volumetric contribution of each dietary item to the total stomach volume (%V). This was done following the point method described by Hyslop (1980). The diet items were identified at the possible low taxonomic level. Each food content in the stomach was allotted one of the number of points - 0, 1, 2, 4, 8 and 16 - based on its volume, from the smallest to the largest value, respectively. Then percentage volumes within each stomach analyzed were then calculated to give the percentage composition in a diet of individual fish species. Also, vacuity index or the stomach emptiness index (VI) of each species was estimated using the equation given by Euzen (1987): VI = (the number of empty stomachs of species *i* / total number of the stomachs of species *i* examined) × 100.

By using the dietary volume data, the standardized Levin's (1968) diet niche breadth (B_a) was estimated for each species in all estuaries following Hurlbert (1978). The following formula was used:

$$B_a = \frac{[(P_{ij}^2)^{-1} - 1]}{(n - 1)}$$

where B_a is the standardized trophic niche breadth, P_{ij} is the proportion of food category *j* in the diet of the species *i* and *n* = total number of food items in the diet of species *i*. The B_a values range between 0, when only one resource is used, and 1, when all resources are used equally. In addition to that, the dietary overlap (*O*) of the predatory fish species in each estuary were estimated by using Pianka's index of niche overlap (Pianka, 1973), which considers that the different dietary resources are equally accessible to all species. The formula used was:

$$O = \frac{\sum P_{ij} P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where P_{ij} and P_{ik} are the proportions of diet category *i* comprised in the diets of *j* and *k*, respectively. Both diet niche breadth (B_a) and overlap (*O*) were considered low when the values fall within 0-0.39 range, intermediate when they are within 0.4-0.6, and high when ranged from 0.61-1.

Overall interspecific variations in the diet of the fish species between and within the two estuaries were assessed by main and pairwise permutation multivariate analysis of variance (PERMANOVA). The multivariate analysis, including cluster analysis that produces dendro-

grams to measure the similarity in diet, and the PERMANOVA tests were run based on the Bray Curtis similarity matrices made from the square root transformed volumetric percentage dietary data using PRIMERv6 with PERMANOVA + add-on module statistical packages (Anderson *et al.*, 2008). Before conducting any statistical test, diet data were subjected to normality and homogeneity of variance tests, the assumptions were not met. Thus, non-parametric method was opted and because of the multiple variables, the multivariate analyses of variance tests were selected.

Stable isotopes and trophic niche indices analyses

For each fish species collected for stomach content analysis, representative samples were selected randomly to extract dorsal white muscle tissues for stable isotope analysis (SIA). The sample size (*n*) and length size (total length - TL - in cm) of each species were different: *A. africanus* from Wami = TL ranged 16.6-29.9 cm (*n*=16); *A. africanus* of Pangani = TL ranged 13.5-44.2 cm (*n*=16); *E. coioides* of Wami = TL ranged 15.3-30.5 cm (*n*=6); *E. coioides* of Pangani = TL ranged 15.6-32.0 cm (*n*=6); *P. argenteus* of Wami = TL ranged 31.3-41.0 cm (*n*=5); and *S. sihama* of Pangani = TL ranged 15.0-25.6 cm (*n*=8). The extracted muscle tissues were oven-dried at 60°C and ground to a powder form. A subsample of each sample was weighed to the nearest 0.9 mg and placed into tin capsules for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ compositions of each sample were determined simultaneously using a dual pumped Sercon model 20-20 Continuous Flow Isotope Ratio Mass Spectrometer (CF/IRMS or EA/IRMS) linked to a Thermo model EA1110 Elemental Analyser (EA). The equipment utilizes dual reaction tubes (combustion/reduction), a magnesium perchlorate drier and a Carbosieve G separation column. Stable isotope results were expressed in the delta notation (δ) relative to the known standards, Vienna Pee Dee Belemnite (VPDB) for $^{13}\text{C}/^{12}\text{C}$ and atmospheric nitrogen for $^{15}\text{N}/^{14}\text{N}$ ratios. The $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ were calculated using the following formula:

$$\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where R is either $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$.

These isotope analyses were carried out at the OEA Labs Limited in the United Kingdom. Before statistical analysis of isotopic results, these latter were evaluated to gauge if the lipid contents were likely to affect the analysis using the C:N ratio (Post *et al.*, 2007). The C:N ratios of all species were below 3.5, thus, in accordance with Post *et al.* (2007), the levels of lipids in tissues of fish samples were not enough to skew isotopic results. To test the variations in isotopic values among fish species and between estuaries, the isotope data were subjected to main and pairwise PERMANOVA tests. Two fixed factors,

species and estuaries, were considered. The tests were run based on the Euclidian distance resemblance matrix made from the normalized isotopic data.

Furthermore, to enable quantitative comparisons of the trophic niche of fish communities within and between the two estuaries, the standard ellipse area corrected for small sample size (SEAc), total convex hull area (TA), and other five Layman metrics were estimated using the Stable Isotope Bayesian Ellipses in R (SIBER, Jackson *et al.*, 2011) package version 4.0.5 (R Core Team, 2021). Standard ellipse area corrected for small sample size and TA and were estimated as quantitative proxies of the isotopic niche width that measure total trophic diversity or niche area. However, these two metrics differ, because SEAc is less sensitive to outliers and sample size, as it is corrected for small sample sizes, than the values of TA. For statistical comparison of SEAc between the communities investigated, the posterior distribution of the Bayesian standard ellipse (SEAb) and the 95% credible intervals (CIs) were calculated (Jackson *et al.*, 2011). To test whether the isotopic niche space of fish population of Wami estuary is larger, smaller or similar to the comparable population of Pangani, the 95% CI of SEAb and TA of those targeted pairs of fish species (see previous paragraphs) were compared. When the CI of distinct pairs of species did not completely overlap, the trophic niche of the comparable populations was significantly different. By following Jackson *et al.* (2011), the probability that SEAb or TA of species of Wami was smaller than that of Pangani was also quantified. The proportions of overlaps for the comparable groups were also calculated using Bayesian Overlap and compared as they had to match with the density plot for the 95% prediction ellipsoids. The overlaps estimated aimed at describing how much of each species' niche overlapped with others between and within the estuaries.

As per Layman *et al.* (2007), other metrics estimated using SIBER package were $\delta^{13}\text{C}$ range (CR), $\delta^{15}\text{N}$ range (NR), mean distance to the centroid (CD), mean nearest neighbor distance (M-NND) and standard deviation (SD) of the M-NND (SD-NND). These Bayesian-derived estimates allow statistical comparisons between communities without any restriction on the number of the groups within the communities (Layman *et al.*, 2012; Donázar-Aramendía *et al.*, 2019). The CR was used to indicate trophic diversity or niche diversification at the base of the food web. The NR was used to infer both trophic diversity and the trophic length, meaning that a larger range infers a wide trophic spectrum. The CD, which is the average Euclidian distance of each community component to the centroid, was used to infer the average degree of trophic diversity. The two metrics, M-NND and SD-NND were used to evaluate to what extent the trophic redundancy of the fish community vary between the estuaries. The M-

NND measures the density of species packing, meaning that species or groups with similar trophic ecologies show smaller values of M-NND and thus represent increased trophic redundancy. The SD-NND metric indicates the evenness of species packing. This means that lower SD-NND is indicative of more even distribution of species, the indicator of higher trophic redundancy as a result of different groups having more similar trophic ecologies (Layman *et al.*, 2007). The SD-NND also show diversification of trophic niches (Donázar-Aramendía *et al.*, 2019).

RESULTS

Diet compositions of predatory fish

A total of 420 stomachs of four estuarine predatory fish species were examined. Out of that, 332 (79%) contained food items that were used for further analyses. Irrespective of where species were caught, seven dietary items were identified in the stomachs of predatory fish species, namely: prey fish, stomatopods, bivalves and other unidentified mollusks, prawns, shrimps, polychaetes and crabs. Digested materials and remains of hard parts of preys were also seen in some species. Detrital materials and sand particles were observed as accidental items ingested by *A. africanus*. At the species level, the values of vacuity index (VI) were considerably high in both estuaries (Table 1) and the patterns of VI showed that the predatory fish species were more voracious in Wami relative to that of the Pangani estuary.

With the exclusion of polychaetes observed in the stomachs of both *A. africanus* and *S. sihama*, as well as detrital materials found only in the stomachs of *A. africanus*, all other preys were common in all four predatory fish species under investigation, albeit with different volumetric contribution (Table 1). *Arius africanus* of Wami estuary fed mainly (by volume) on bivalves (27%) followed by other mollusks (26%) and small fish (19%), while *A. africanus* of Pangani estuary ingested large amounts of bivalves (36%), other mollusks (31%) and crabs (9%). Stomatopods and shrimp prey were rarely seen in the stomachs of *A. africanus* from Wami estuary. Fish prey, prawns and crabs were the three most consumed preys equally by *E. coioides* in the Wami estuary, whereas prawns, fish, and stomatopods occupied large percentage of diet for individuals caught in Wami estuary (Table 1). The diet of *P. argenteus* of Wami estuary was mainly dominated by prawns and to some extent by fish and mollusks, while *S. sihama* of Pangani estuary ingested large amounts of fish, shrimps, and substantial amounts of polychaetes (Table 1). Despite grouping the prey types at higher taxonomic level, it was noticed that *Valamugil spp.* were dominant among the fish preys encountered in the stomachs of all the fish examined.

Multivariate analyses of dietary composition in predatory fish

The dendrogram prepared based on the volume of prey items showed that the diet items consumed by the population of *A. africanus* of Wami and that of the Pangani estuaries were highly similar for about 75% (Figure 2). It was

also revealed that about 50% of the diet of *E. coioides* of Wami was shared with *P. argenteus* from the same estuary (Figure 2). The prey items consumed by *E. coioides* population of Wami were to some extent different (about 40% similarity) to that of the population of Pangani estuary. The results further highlighted that the preys consumed by Pangani-drawn *E. coioides* and *S. sihama* were far related (40%

Table 1. Diet composition of *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* found in their stomachs and dietary indexes of each prey item: frequency of occurrence (%F), percentage volumetric contribution (%V), number of stomachs with food/content (n) and vacuity index percentage (%VI).

Food items	Wami estuary						Pangani estuary					
	<i>A. africanus</i> (n = 48)		<i>E. coioides</i> (n = 52)		<i>P. argenteus</i> (n = 54)		<i>A. africanus</i> (n = 74)		<i>E. coioides</i> (n = 52)		<i>S. sihama</i> (n = 52)	
	%FO	%V	%FO	%V	%FO	%V	%FO	%V	%FO	%V	%FO	%V
Fish	50.0	19.4	51.6	22.4	31.1	11.6	20.8	7.6	64.7	23.2	45.7	33.7
Stomatopods	2.4	1.2	51.6	11.9	13.3	4.0			64.7	19.4	2.9	2.6
Bivalves	42.9	27.0	9.7	1.5	26.7	9.0	58.3	35.7				
Other mollusks	40.5	26.0			26.7	10.1	62.5	31.2	35.3	8.8	22.9	13.1
Prawns			51.6	22.1	84.4	54.1	16.7	4.8	70.6	32.1		
Polychaetes	19.1	5.7					20.8	6.5			22.9	17.1
Crabs	35.7	12.0	64.5	22.4	26.7	8.0	31.3	9.3	35.3	12.1	5.7	1.5
Shrimps	14.3	3.6	41.9	14.8					11.8	4.4	28.6	20.6
Sand/detritus	4.8	3.0					2.1	1.0				
Hard tissues/parts			19.4	3.9	2.2	0.9	6.3	1.9				
Unidentifiable/digested	18.1	2.1	6.5	1.0	15.6	2.3	14.6	1.9			25.7	11.4
Vacuity index (VI)		9.76		21.21		15.63		22.58		33.33		23.56

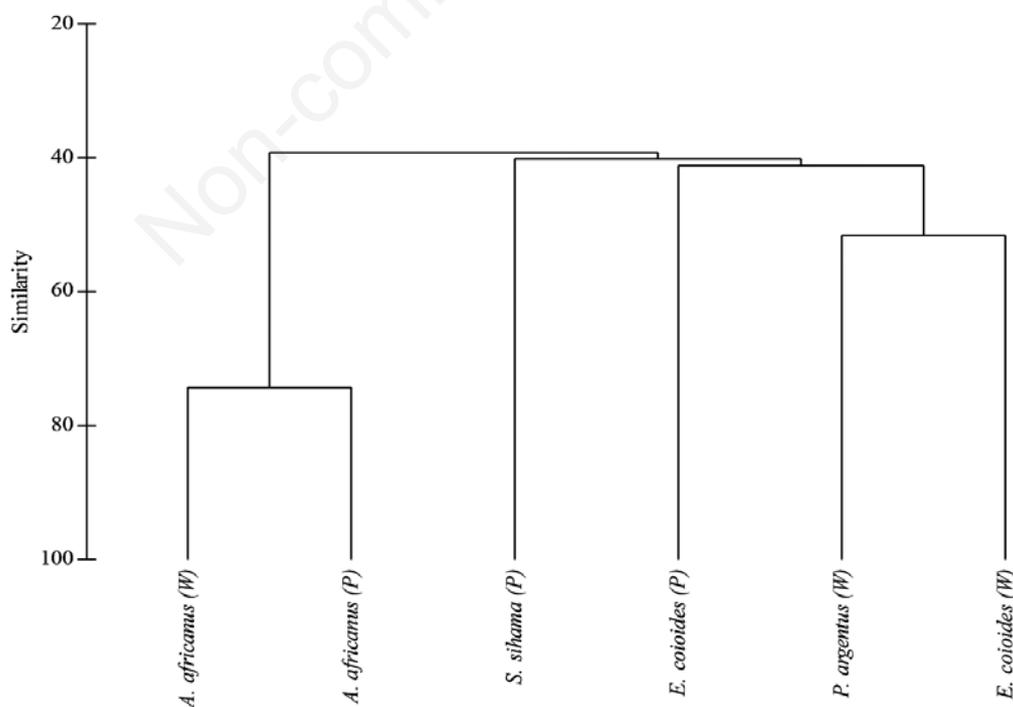


Figure 2. Dendrogram for hierarchical clustering of dietary composition (by percentage volume) in *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* collected from Pangani (P) and Wami (W) estuaries.

average similarity) to each other. The low levels of similarity in prey consumed by fish were also seen among the *E. coioides*, *A. africanus* from the two estuaries and *P. argenteus* drawn from Wami estuary (40% average similarity, Figure 2). The results of PERMANOVA test paired with that of dendrogram showed significant differences among species (Pseudo- $F=21.0$; $p=0.001$; Table 2) as well as the interactions between main factors, species, and estuaries (Pseudo- $F=21.0$; $p=0.001$; Table 2). Even the pairwise PERMANOVA tests indicated spatial intra-specific diet variations of each of the three pairs of predatory fish species caught from Wami and Pangani estuaries ($t \geq 1.88$; $p \leq 0.05$; Table 3).

Dietary niche breadth and overlaps of predatory species

The values of index of dietary niche breadth (Ba) of the predatory fish species varied from 0.29 to 0.7 (Figure 3). Despite the dietary volume of *E. coioides* varied between estuaries (Table 2), the species presented much higher values of Ba as compared to other species (Figure 3). *Arius africanus* from Wami showed moderate niche breadth, whereas specimens from Pangani estuary showed lower values of Ba (Figure 3). A different situation was noticed for the comparable pair of *P. argenteus* from Wami and *S. sihama* from Pangani where the former species showed lower, and the latter species showed moderate dietary niche breadths (Figure 3). Furthermore, the analysis of dietary overlaps based on Pianka's index (O) revealed much high values ($O > 0.6$) for the following pairs: *A. africanus* of Wami and *A. africanus* of Pangani, *E. coioides* of Wami and *E. coioides* of Pangani, as well as *P. argenteus* of Wami and *E. coioides* of Pangani, (Table 4) which is an indication of low trophic flexibility of these species in two estuaries. However, the lowest index of overlap ($O=0.2$) was presented by the pair of *P. argenteus* of Wami versus *S. Sihama* of Pangani (Table 4).

Variations in stable isotopes of predatory fish and their representative prey fish

It was revealed that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios were significantly different among species and between estuaries (PERMANOVA, Pseudo- $F=27.3$, $p=0.001$; Table 5 and Figure 4). Moreover, there were significant interactions

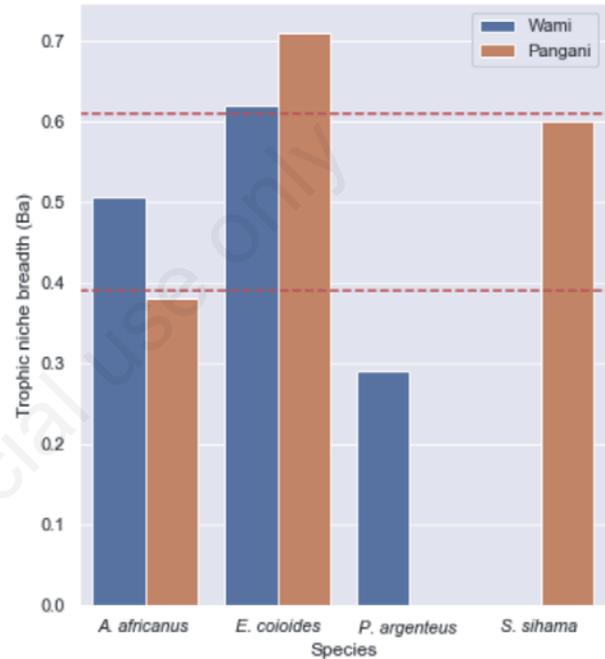


Figure 3. Index of dietary niche breadth (Ba) of predatory fish species, *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* collected from Wami and Pangani estuaries. The dotted line indicates the classes of the Ba , 0 – 0.39 = low Ba ; 0.4 – 0.6 = moderate Ba and 0.61 – 1 = high Ba .

Table 2. Two-way PERMANOVA of diet composition in predatory fish species of *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* from Wami and Pangani estuaries. Sq.root CoV = square root component of variation.

Source of variation	df	MS	Pseudo- F	p (perm)	Sq. root CoV
Estuary	1	10257	4.0	0.002	11.43
Fish species	3	53316	21.0	0.001	33.23
Estuary x Fish species	1	7927.5	3.1	0.012	23.51
Residual	213	2538			50.38

Table 3. Pair-wise PERMANOVA of spatial variations in diet composition of *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* from Wami and Pangani estuaries.

Estuary comparisons of fish species	Denominator df	t	p
<i>A. africanus</i> (W) and <i>A. africanus</i> (P)	88	1.88	0.02
<i>E. coioides</i> (W) and <i>E. coioides</i> (P)	46	2.03	0.01
<i>P. argenteus</i> (W) and <i>S. sihama</i> (P)	88	4.17	0.001

between species and estuaries (PERMANOVA, Pseudo- $F=22.6$, $p=0.001$; Table 5). At spatial scale, the individual predatory fish species exhibited a clear distinction of isotopic values between estuaries (Figure 4 and Table 6). As such, the mean isotope ratio of *A. africanus* ($-17.3\pm 1.2\text{‰}$;

$13.3\pm 0.3\text{‰}$) and *E. coioides* ($-18.6\pm 0.7\text{‰}$; $13.6\pm 0.5\text{‰}$) of Wami estuary were significantly lower in terms of $\delta^{13}\text{C}$ but higher in terms of $\delta^{15}\text{N}$ ratios when compared to that of Pangani estuary (-16.3 ± 2.1 ; $11.1\pm 1.8\text{‰}$; $-18.0\pm 0.7\text{‰}$, $12.8\pm 0.6\text{‰}$) (Figure 4 and Table 6; Pair-wise PER-

Table 4. Niche overlaps between pairs of predatory fish species analyzed from Wami (W) and Pangani (P) estuaries.

Species	<i>A. africanus</i> (W)	<i>E. coioides</i> (W)	<i>P. argenteus</i> (W)	<i>A. africanus</i> (P)	<i>E. coioides</i> (P)	<i>S. sihama</i> (P)
<i>A. africanus</i> (W)		0.42	0.33	0.94	0.42	0.58
<i>E. coioides</i> (W)			0.34	0.25	0.97	0.56
<i>P. argenteus</i> (W)				0.37	0.84	0.21
<i>A. africanus</i> (P)					0.31	0.30
<i>E. coioides</i> (P)						0.49
<i>S. sihama</i> (P)						

Table 5. Two-way PERMANOVA results on isotopic variation of predatory fish species at species and estuary level for *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* from Wami and Pangani estuaries.

Source	df	MS	Pseudo-F	P(perm)
Fish species	3	20.85	27.234	0.001
Estuary	1	12.43	16.242	0.001
Fish species x estuary	3	17.30	22.606	0.001
Residual	95	0.766		

Table 6. Pair-wise PERMANOVA results of intraspecific variations in stable isotopes composition of *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* between Wami and Pangani estuaries.

Estuary comparisons of fish species	Denominator df	t	p
<i>A. africanus</i> (W) and <i>A. africanus</i> (P)	30	4.37	0.001
<i>E. coioides</i> (W) and <i>E. coioides</i> (P)	16	2.61	0.004
<i>P. argenteus</i> (W) and <i>S. sihama</i> (P)	23	8.58	0.001
<i>V. buchanani</i> (W) and <i>V. buchanani</i> (P)	26	1.03	0.363

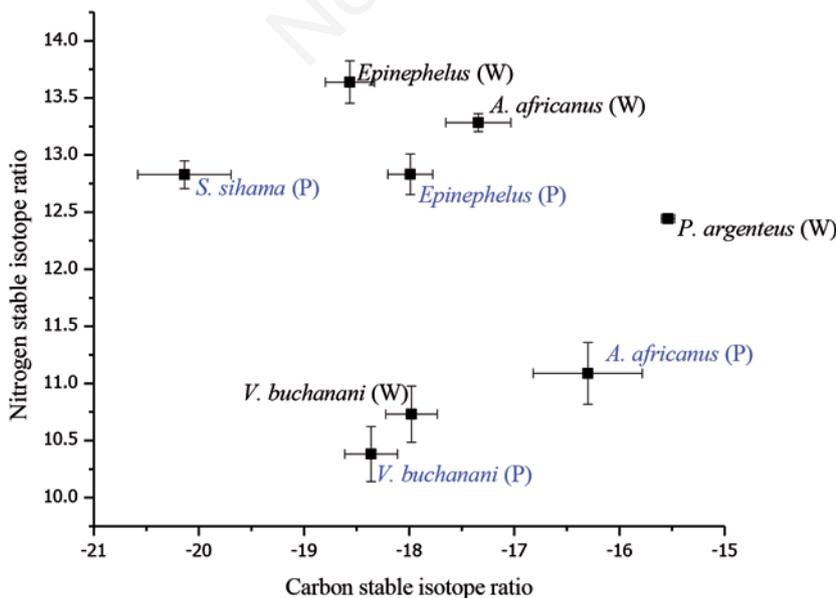


Figure 4. Bi-plot of mean and standard error (SE) of carbon and nitrogen stable isotopes of *Arius africanus*, *Epinephelus coioides*, *Pomadasys argenteus* and *Sillago sihama* and their main prey fish *Valamugil buchanani* from Wami and Pangani river estuaries.

MANOVA, $t=4.4$, $p \leq 0.004$). Similarly, the stable isotope ratio of *S. sihama* based in Wami when compared with *P. argenteus* of Pangani, were significantly variable. This meant that the isotopic ratios of *S. sihama* of Pangani estuary exhibited the lowest $\delta^{13}\text{C}$ ($-20.1 \pm 1.7\text{‰}$) and higher $\delta^{15}\text{N}$ ($12.8 \pm 0.5\text{‰}$) values when compared to that of *P. argenteus* from Wami estuary ($-15.5 \pm 0.2\text{‰}$, $12.4 \pm 0.1\text{‰}$; Figure 4). For the potential prey-fish, *V. buchanani* despite the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values being slightly higher in Wami compared to that of Pangani (Figure 4), the isotopic variations were statistically not significant (pairwise PERMANOVA, $t=1.03$, $p > 0.05$; Table 6).

Isotopic trophic diversity, niche width and overlaps of fish populations

The CR (that measures the trophic diversity) and NR (measuring trophic length and diversity) of *A. africanus* were shorter in the Wami estuary compared to that of the Pangani estuary (Table 7). The situation was also similar

for other metrics of trophic niche width of *A. africanus*, such as the Bayesian estimate of trophic niche width (SEAb) and SEAc (Figure 5 and Table 7). Likewise, the same trend was also noticed for the SEAb and SEAc of the other three pairs of species of comparison from Wami and Pangani estuaries (Figure 5 and Table 7). The results of the intra- and interspecific comparisons of SEAb within and between the estuaries varied from one pair to another of predatory species. The SEAb of *A. africanus* from Wami was significantly smaller than that of Pangani estuary with no intraspecific overlap in between Bayesian estimate of 95% CI (Table 7). This was also in line with estimate of the probability of SEAb of less than 1% for the *A. africanus* based in Pangani to be smaller than that of Wami estuary (Table 7). The SEAb of *E. coioides* from both Wami and Pangani estuaries were statistically similar to each other due to large overlaps between 95% CI and 50% in magnitude of probability of the SEAb for the two pairing species (Table 7). Even CR and NR of *E. coioides*

Table 7. Bayesian standard ellipse area widths (SEAb), magnitude of probability of SEAb for the Wami-based species to be smaller than Pangani based estuarine species; SEAc, CR and NR for *A. africanus*, *E. coioides*, *S. sihama*, *P. argenteus* and *V. buchanani* studied in Wami and Pangani estuaries. CI – credible interval of 95%.

Species	Wami			Pangani			Probability (%) of SEAb for species of Wami < Pangani for 95%CI
	%CI	Lower	Upper	%CI	Lower	Upper	
<i>A. africanus</i>	99	0.59	2.31	99	1.99	8.04	0.0005
	95	0.68	1.92	95	2.36	6.67	
	50	0.95	1.35	50	3.20	4.60	
	Mode	1.11			3.81		
	SEAc	1.26			3.69		
	CR	3.56			7.00		
	NR	0.92			3.44		
<i>E. coioides</i>	99	0.37	3.09	99	0.44	2.86	
	95	0.47	2.27	95	0.56	2.20	
	50	0.78	1.29	50	0.89	1.38	
	Mode	1.00			1.09		
	SEAc	1.27			1.32		
	CR	1.86			1.51		
	NR	1.50			1.46		
<i>P. argenteus</i> (Wami)/ <i>S. sihama</i> (Pangani)	99	0.02	0.11	99	0.84	4.03	50
	95	0.02	0.09	95	0.99	3.20	
	50	0.04	0.05	50	1.49	2.18	
	Mode	0.04			1.81		
	SEAc	0.05			1.98		
	CR	0.61			4.38		
	NR	0.26			1.52		
<i>V. buchanani</i>	99	0.87	4.36	99	1.34	5.89	-
	95	1.06	3.53	95	1.67	4.77	
	50	1.57	2.35	50	2.39	3.37	
	Mode	1.91			2.85		
	SEAc	2.18			3.19		
	CR	2.4			2.98		
	NR	2.55			2.56		

from these estuaries were relatively similar. The SEAb, and thus, trophic niche width, of *S. sihama* of Pangani was significantly larger as compared to that of *A. argenteus* of Wami due to zero overlap between the 95% CI (Table 7). Contrary to that, the substantial overlap between the 95% CI for the *V. b Buchananani* from both Wami and Pangani estuary (Table 7) was considered as an indication that the trophic niche width of the species in these habitats is somewhat similar. Furthermore, the SEAb between the following pairs of species were also significantly different when their 95% CIs were compared: both pairs of *A. Africanus* versus *E. coioides* from within Pangani and Wami estuaries, *E. coioides* versus *P. argenteus* of Wami as well as *A. Africanus* versus *P. argenteus* of Wami estuary (Table 7). Similar to *A. africanus*, the CR and NR of *S. sihama* (CR=4.4‰, NR=1.5‰) and *V. b Buchananani* (CR=3.0‰, NR=2.6‰) were consistently higher in Pangani estuary than those of their comparable species in the Wami estuary (*P. argenteus* CR=0.6‰, NR=0.3‰; and *V. b Buchananani* CR=2.4‰, NR=2.5‰; Figure 5 and Table 7).

The SEAc showed substantial overlap between the standard ellipses for *A. africanus* and *E. coioides* from Wami estuary, and between all comparable species from Pangani estuary (Figure 5). This indicated that the degree of dietary resource sharing by predatory fish was higher in Pangani compared to that of Wami estuaries. Specifically, the estimates of SEAc overlap analyses revealed that, in Wami estuary, the percentage of overlap between SEAc for *A. africanus* onto that of *E. coioides*, and vice versa, was 54%. No overlap of SEAc was found between *A. africanus* versus *P. argenteus* nor *E. coioides* versus *P. argenteus* from Wami estuary. Contrary to that, in Pangani estuary, the largest percentages of overlap were indicated by SEAc for the *S. sihama* onto that of *A. africanus* (62%) and for the *E. coioides* onto that of *A. africanus* (61%). The percentage of SEAc for the *A. africanus* versus *E. coioides* was 21% and *A. africanus* versus *S. sihama* was 34%. More so, the percentage of *E. coioides* that overlapped with *S. sihama* was 58%, while that of *S. sihama* onto the SEAc of *E. coioides* was 16%. The results of intra-specific overlap between estuaries indicated that the SEAc for the *A. africanus* of Pangani onto that of Wami was 11%, but the values of the overlap for the vice versa was 33%. For the *E. coioides*, the overlap percentages between estuaries were 57% and 59%. Again, there was no ellipse overlap for the *P. argenteus* of Wami and *S. sihama* of Pangani.

Trophic niche and redundancy at estuary level

The SEAc and TA that infer the total trophic niche area of fish community were smaller in Wami (SEAc=5.4; TA=14.6) contrary to that of Pangani estuaries (SEAc=7.6; TA=25.1; Figure 6). The comparison test for the Bayesian estimate 95% CI of the two estuaries re-

vealed that SEAb of Wami was slightly smaller than that of Pangani as they showed substantial overlap between the 95% CI (Wami estuary 3.90-6.94 of 95% CI; Pangani estuary 5.70-9.69 of 95% CI). However, the magnitude of probability for SEAb of Pangani to be smaller than that of Wami was impossible to occur (<1%). More so, the high level of overlap between SEAc of two estuaries was noticed whereby the SEAc of Wami was greatly enclosed within that of Pangani estuary (Figure 6).

As well, the Layman community indices showed that the two estuaries differ in trophic resources and level of trophic diversifications of the same fish species investigated (Figure 7). The trophic length as indicated by the NR of Pangani estuary (NR=2.45) was marginally shorter when correlated with that of Wami (NR=2.91; Figure 7). The opposite situation was noticed for the indicator of

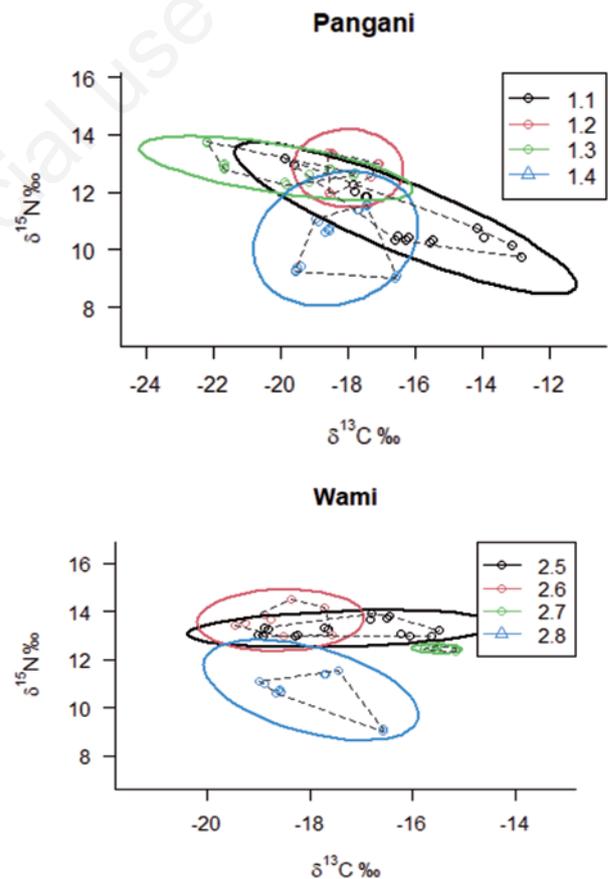


Figure 5. The convex hull area (dotted lines) and standard ellipse areas (SEA) measuring the trophic niche width of individual predatory fish: 1.1 *Arius africanus* from Pangani; 2.5 *A. africanus* of Wami; 1.2 *Epinephelus coioides* of Pangani; 2.6 *E. coioides* of Wami; 1.3 *Sillago sihama* of Pangani; 2.7 *Pomadasys argenteus* of Wami and their prey fish; 1.4 = *Valamugil b Buchananani* from Pangani and 2.8 = *V. b Buchananani* of Wami and Pangani estuaries.

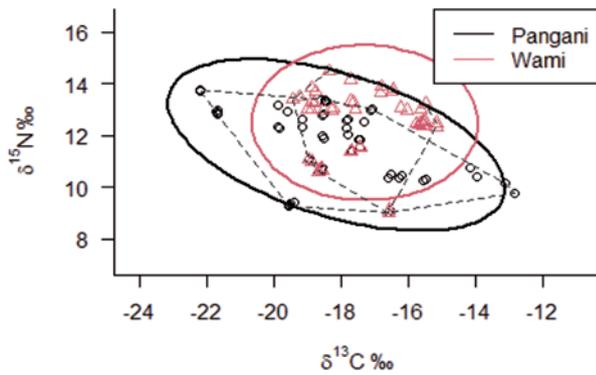


Figure 6. Trophic niche width indicated by TA (dotted lines) and SEA (solid lines) for the pooled stable isotopes of carbon and nitrogen of fish from Wami and Pangani estuaries ($n = 103$). Cycle points represent individuals of all the species measured in each estuary and standard ellipse/circle represent the maximum likelihood of isotopic niche of the species analyzed.

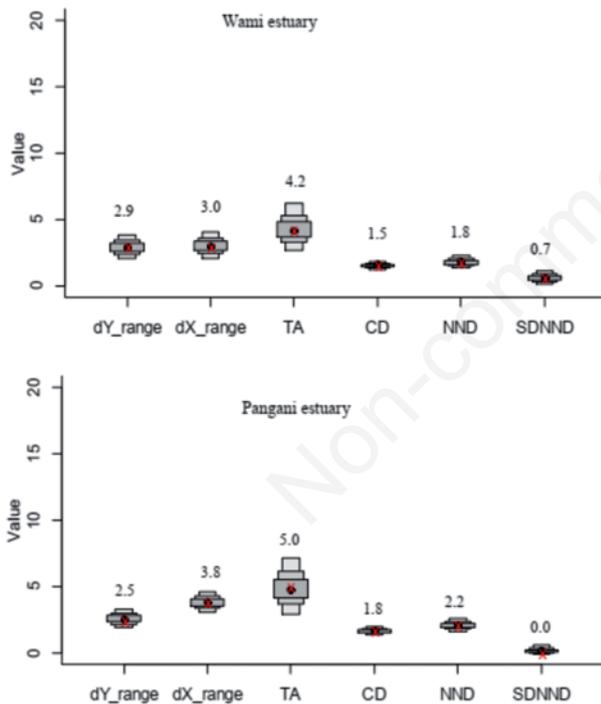


Figure 7. The estuarine community-wide Layman metrics of Wami and Pangani estuaries that showed the (i) trophic length, or complexity, NR (dY_range), (ii) trophic diversity, or CR (dX_range), (iii) niche width, or convex hull area (TA), (iv) average trophic diversity, or mean distance to the centroid (CD), (v) trophic redundancy, or the mean nearest neighbor distance (NND), and (vi) evenness of species packing, or extent of trophic diversification, that is, the standard deviation ($SDNND$). Black dots are the modes, boxes indicate the credible intervals at 50%, 75% and 95%. The numbers above each box are modes; the cross (red) is the values of the true population.

basal and average trophic diversity of fish as expressed by the CR and CD (Figure 7). The trophic redundancy (measured as M-NND) and its standard deviation (SDNND) differed substantially between the two estuaries with M-NND being smaller and SDNND larger in Wami than Pangani estuary (Figure 7).

DISCUSSION

The findings of this study indicate how anthropogenic activities in the upstream of the river catchments induce changes to the estuarine ecosystem's functioning. The results suggest that despite the Wami estuary being under conservation status, the high level of disturbances upstream of the river increase vulnerability of the estuarine food web structure and ecosystems functioning. This is probably connected to a lower primary production, to changes in trophic positions of consumers, and thus to modifications occurring in the trophic niche of the predatory fish. As a result, the reduced trophic diversity, ecological redundancy, and complexity of the ecosystem are most likely experienced in Wami estuary than Pangani estuary. This was different from the expectation as the considered highly disturbed Pangani estuary presented a relatively stable, resilient, and ecologically redundant ecosystem.

Even though our findings are based on few components of the estuarine food webs, they include important compartments that greatly shape the complexity and thus determine the ecological redundancy of the estuarine ecosystems of concern. Furthermore, the inferences drawn from the present study are based on data collected in a specific seasonal period, so that isotopic values gathered from estuarine fish with large body size (*i.e.*, predatory fish) mirror the exploitation of natural resources during their growth period. Moreover, data collection that adheres to seasons may elucidate more on long-term changes in the use of dietary resources and other niche characteristics of estuarine fish assemblage. Moreover, our results explain how both predatory and prey fish respond to the dynamics of dietary resources, representing with a good approximation the food web state in tropical estuaries differing in the degree of anthropogenic disturbances.

Our findings showed that both stomach contents and stable isotopes can reveal significant differences in diet and isotopic values among fish species in different estuaries. Matching of these findings confirm that both methods can characterize the foraging flexibility of predatory fish species of marine origin in estuaries. Except for *A. africanus*, the results of the index of dietary niche breadth, *Ba*, have matched well with that of isotopic trophic niche metrics of the species between estuaries. As such, the observed consistent highest *Ba* of *E. coioides* in both estuaries correlated with the similarity in their SEAb between

estuaries. Similarly, the estimated moderate Ba of *S. sihama* from Pangani and the lowest Ba of *P. argenteus* from Wami correlated with the larger SEAb of Pangani-based *S. sihama* versus the comparable smaller SEAb of *P. argenteus* of Wami estuary. However, the mismatch of trophic feeding niche of *A. africanus* by the two methods indicates that the trophic dynamics in highly fluctuating estuarine ecosystems requires robust methods that should complement the conventional stomach content analysis for drawing a sound and logical conclusion. The application of stable isotope in trophic ecology studies is widely accepted (*e.g.* Pasquaud *et al.*, 2010; Olsen *et al.*, 2011; Layman *et al.*, 2012; Cummings *et al.*, 2012) as it is among the powerful tools that ensure the determination of the integrated diet consumed and assimilated at a coarse taxonomic scale but over a long period (Michener and Lajtha, 2007; Selleslagh *et al.*, 2015). Relative to that, the stomach content analysis determines the diet ingested instantly by the consumers at a finer taxonomic level (Mahesh *et al.*, 2018).

The marked variations in the dietary composition and trophic niche among the predatory fish species found in our study imply that they largely consume similar preys but in different proportions in the two estuaries. Differences in the amounts of preys consumed may be linked to the prey abundance and catchability along with prey visibility by predatory species, plus the feeding strategies and energy requirements (Kulbicki *et al.*, 2005; Kroetz *et al.*, 2016). Both stomach contents and stable isotope-derived Layman metrics showed a considerable degree of trophic resource sharing and thus trophic niche overlaps among these predatory fish in estuaries. This finding agrees with those from the study of Matich *et al.* (2017). This possibly does not imply competition in trophic resources but rather the prey-catch strategies that define the prey types consumed. For instance, the higher trophic niche breadth and similarity in isotopic niche width of *E. coioides* in Wami and Pangani estuaries could be favored by its ambush strategy and structural complexity of the estuaries (Gibran, 2007). Complex habitats such as these mangrove-sheltered estuaries provide enhanced cover that reduces the possibilities of predators to be detected by the preys (Mwijage *et al.*, 2018a). This situation is probably connected with the highest overlap of SEAc of the species between estuaries.

Inter- and intra-species variations in isotopic values could mean considerable individual variability in the feeding strategies with individuals consuming prey of different trophic spectra and the use of basal nutritional sources they rely on. Differences in both dietary niche breadth and isotopic niche width at the estuary level suggest that fish species may have high trophic niche plasticity or flexibility, which is indicated by Matich *et al.* (2017) as a mechanism to respond to natural and human-induced

environmental change. This is further indicated by the dissimilarity in magnitude of the isotopic metric-based overlap of each possible pair of the predatory fish species in the two estuaries examined. The highest degree of overlap for the fish species of Pangani might be an indication of shifts in the trophic positions of organisms preyed upon by these species in two estuaries resulting to the observed differences in trophic length, diversity and trophic niches justified by NR, CR, CD and SEAc/SEAb. The shifts in trophic positions of consumers within comparable aquatic environment is mainly driven by differences in individual diet, trophic discrimination or enrichment factor (Villamarín *et al.*, 2018), as well as differences in the level of nutrients load fueling the base of the food web (Warry *et al.*, 2016).

Furthermore, our findings suggest a possibility of presence of ontogenetic shift in trophic positions (Park *et al.*, 2018; Villamarín *et al.*, 2018) for the comparable estuaries examined herein. Although the length size of the individuals was not considered during analysis, it might also influence the results of the differences in isotopic values of the species between the estuaries. This is mainly linked with the size range (total length, TL) of *A. africanus* from Wami versus of Pangani and *P. argenteus* of Wami versus *S. sihama* of Pangani. The literatures emphasize that resource utilization patterns of fish change markedly with ontogeny (Davis *et al.*, 2012; Park *et al.*, 2018; Villamarín *et al.*, 2018).

Specifically, with the exclusion of *E. coioides*, the larger CR of predatory fish populations of Pangani estuary might be linked with their prey to feed on the diet with varied nutritional sources. The largest SEAb of *A. africanus* population of Pangani could be probably associated with a high level of opportunistic or generalist feeding mechanism as a coping strategy resulting from exposing the estuary to more frequent human perturbations. The smallest SEAb of *P. Argenteus* of Wami and its $\delta^{13}\text{C}$ mean values ($-15.5 \pm 0.2\%$) is an indication that the riverine or terrestrial derived dietary sources of which their $\delta^{13}\text{C}$ ratio range from -23 to -30% (Bouillon *et al.*, 2011) had little influence on the diet dynamics of this species. This is somewhat contributed by the sampling location of the samples. *Pomadasys argenteus* was caught in the estuarine plume away from the river mouth, and this environment might have been less influenced by the riverine dietary sources. The same situation further explains the observed non-overlap of SEAc between *P. Argenteus* and any other pair of predatory fish studied. More so, the similarity in SEAb of *E. coioides* between estuaries suggests low trophic niche flexibility of the species. In view of that situation, the environmental filtering hypothesis plays a role in this assembly that was not similar due to divergence in the environmental conditions of the species habitats (Pereira *et al.*, 2017).

Furthermore, the higher values of $\delta^{15}\text{N}$ and NR of Wami-associated species may be an indication of the predatory fish to occupy higher trophic position usually connected to the nature of the diet assimilated by individuals, the trophic enrichment factor and high levels of nutrients load (Villamarín *et al.*, 2018), as opposed to Pangani estuary. The effects of high values of $\delta^{15}\text{N}$ at low trophic level are transmitted upwards higher up to top predators of estuarine food web, thus affecting the overall trophic organization (Warry *et al.*, 2016). Parallel to this, the substantial low $\delta^{13}\text{C}$ ratio could be contributed by the Wami estuarine food web to be fed by riverine primary food sources and high inorganic nitrogen load that elevate $\delta^{15}\text{N}$ values in secondary production (Michener and Lajtha, 2007; Woodland and Secor, 2011; Warry *et al.*, 2016). In the Pangani estuary, water abstractions upstream of the river due to multi-reservoirs for hydropower generation and irrigation is linked with trophic interactions downstream the estuarine and coastal food webs (Mwijage *et al.*, 2018b). These human activities contributed to modify the nutrients' biogeochemistry in the estuary and increased retention time of sediment, organic particles and accompanied nutrients in the reservoirs, upstream of Pangani river (Selemani *et al.*, 2017). Eventually, Pangani estuary experience lower $\delta^{13}\text{C}$ values of terrestrial derived basal food sources (Mwijage *et al.*, 2018a) and regulated nutrients load including nitrogen compounds.

At the estuarine level, the differences in mean distance to the centroid (CD) and SEAc of the Wami and Pangani fish species may be linked to the variations in estuarine primary productivity. The high loads of suspended sediments in the Wami estuary as reported by Kiwango *et al.* (2015) contribute to reducing trophic diversity and abundance resulting from the low rate of aquatic primary production (Selemani *et al.*, 2017). Light penetration is constrained by the suspended particles that, consequently, limit photosynthetic activities. In that way, trophic web connectance, or the number of trophic links to the primary producers, tend to be small. This also may be a factor contributing to the low level of trophic overlap of Wami and consequently, low trophic redundancy (de Carvalho *et al.*, 2017; Lira *et al.*, 2018). The overall effect is to make food web components vulnerable to secondary extinctions as a result of the reduced complexity of the ecosystem (Lira *et al.*, 2018). This supports our findings but not what was expected of Wami to exhibit higher trophic redundancy than Pangani. As such, Wami estuary presented a large SD-NND which suggests a reduced trophic redundancy. This is in contrast to the Pangani estuary that according to Hellar-Kihampa *et al.* (2013), have relatively low sediment loads as large volumes are retained in the dams located upstream of the estuary. This concurred with the findings of Abrantes *et al.* (2014) who reported that the high sediment loads affect aquatic primary productivity

and hence small SEAc of fish populations and communities in the Betsiboka and Tana estuaries.

The predatory fish assemblages in the Wami estuary are probably less opportunistic in feeding that implies a low level of resilience upon disturbances. Selleslagh and Amara (2014) also showed that fish in the Canche Estuary showing very low anthropogenic pressure, exhibited a specialist feeding strategy. The resilience of the estuarine ecosystem is contributed by among others, trophic complexity or multiplicity of trophic linkages along the trophic web and species diversity (Lira *et al.*, 2018). In that sense, the present study agreed with the findings of Pasquaud *et al.* (2010) and Donázar-Aramendía *et al.* (2019) who showed that high degrees of anthropogenic pressures modify the structural components and ecological roles of the species in estuarine ecosystems.

Structural modifications in Wami estuary are certainly influenced by the high turbidity that, apart from affecting primary production, hampers species of higher-order consumers or predatory fish because of lower performances in prey hunting. The reduction of predatory fish species from a community lead to the dominance of its prey at the lower trophic level and subsequent secondary extinctions of other carnivores (Sanders *et al.*, 2018). This also leads to a reduction in trophic redundancy and consequently complexity and stability of the estuarine food webs. On the other hand, the large degree of overlaps in the isotopic niche of species from the Pangani estuary could not imply the existence of potential competitions of the trophic resources but rather the similarity in environmental conditions in microhabitats the fish species used for feeding. Greater diet overlaps increase trophic redundancy of the ecosystem (Sanders *et al.*, 2018), a contention that seems to agree with our results which show that the Pangani estuary has greater trophic redundancy than that of Wami.

CONCLUSIONS

Overall, the community-wide metrics derived from stable isotopes when complemented with dietary data elucidate how predatory fish and their prey respond to human-induced changes in trophic niche width; this response determines cascading effects that impact the trophic redundancy and complexity of the estuarine ecosystems. Our findings indicate that anthropogenic activities in the upstream modified higher trophic position of fish consumers in Wami relative to that of Pangani estuaries. Thus, without management interventions, food web structure reorganization and disruption are likely to occur within the above-mentioned estuaries. Moreover, our findings should be taken with the caveat that not all components of the estuarine food webs were used to draw such inferences, but they could be used as indicators of showing that the two estuarine systems investigated are ecologically disturbed

by anthropogenic activities. Therefore, management initiatives should be strengthened for maintaining the structures and functioning of these fragile ecosystems.

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